

black, the third antennal joint less widely and abruptly dilated, &c.

Elasmogaster unicolor, sp. n.

Pale uniform greyish brown, somewhat coarsely rugulose; antennæ with the first, second, and third joints subequal in length (fourth joint mutilated); membrane almost reaching the apex of the abdomen, the lateral margins of which are widely dilated; rostrum almost reaching the anterior coxæ.

Long., ♂ 17; max. lat. abd. 9 millim.

Hab. East Africa, Nyassa (*Cotterell*).

Differing from *E. africanus*, Dall., the only other described species of the genus, by the pale uniform colour, thus strongly contrasting in the markings of the body, legs, rostrum and antennæ, &c.

Homæocerus Wealei, sp. n.

Reddish ochraceous, body beneath and legs somewhat paler; lateral angles of the pronotum strongly and subacutely produced; lateral margins of the abdomen dilated and directed upwardly; antennæ with the basal joint longest, second joint a little longer than the third or fourth, which are subequal in length; pronotum, scutellum, and corium with coarse brown punctures; extreme lateral edge of the abdomen above ochraceous; membrane pale shining brown; rostrum with the second joint a little longer than the third and subequal in length with the fourth joint.

Long. 14-15; lat. pronot. angl. 5 millim.

Hab. South Africa (*M. Weale*); East Africa, Zanzibar.

This species appears to find a systematic position between the *H. dilutus*, Stål, and *H. productus*, Stål. To the first it is allied by the dilated abdomen, to the second by the produced pronotal angles.

XXIV.—*The Origin of the Organs of Salpa.*

By W. K. BROOKS*.

The Salpa Embryo.—Stated in a word, the most remarkable peculiarity of the Salpa embryo is this—It is blocked out in follicle cells, which form layers and undergo other changes which result in an outline or model of all the general

* From the 'Johns Hopkins University Circulars,' vol. xii. no. 106, pp. 93-97. An abstract of Chapter XIV. of 'A Memoir on the Genus *Salpa*,' which is now in the press.

features in the organization of the embryo. While this process is going on the development of the blastomeres is retarded, so that they are carried into their final positions in the embryo while still in a very rudimentary condition.

Finally, when they have reached the places which they are to occupy they undergo rapid multiplication and growth, and build up the tissues of the body directly, while the scaffolding of follicle cells is torn down and used up as food for the true embryonic cells.

No other animal presents us with an embryonic history quite like that of *Salpa*, although other *Tunicata* show something similar but very much less pronounced. In the chapter of my memoir "On the Morphological Significance of the *Salpa* Embryo," I attempt to show how the life-history of *Salpa* has come about, but we must now confine ourselves to the facts.

An imaginary illustration may help to make the subject clear. Suppose that while carpenters are building a house of wood, brickmakers pile clay on the boards as they are carried past, and shape the lumps of clay into bricks as they find them scattered through the building where they have been carried with the boards. Now, as the house approaches completion, imagine that bricklayers build a brick house over the wooden framework, not from the bottom upwards, but here and there, wherever the bricks are to be found, and that, as fast as parts of the brick house are finished, the wooden one is torn down. To make the analogy more complete, however, we must imagine that all the structure which is removed is assimilated by the bricks, and is thus turned into the substance of new bricks to carry on the construction.

Salensky ("Neue Untersuchungen," &c., *Naples Mittheilungen*, i., 1882, and "Embryonalentwicklung der *Pyrosoma*," *Zool. Jahrb.* iv. and v., 1891) has discovered and minutely described the migration of the follicle; but he has failed to trace the history of the blastomeres, and believes that these degenerate and disappear, and that the embryo is built up of follicle cells. I find that all the follicle cells are ultimately used up as food, and that the true embryo is formed from blastomeres after the analogy of the rest of the animal kingdom.

The Aggregated Salpæ.—During their development the aggregated *Salpæ* undergo complicated changes of position, which render the interpretation of sections very difficult, and as both Salensky (*Morph. Jahrb.* 1877, iii.) and Seeliger (*Jena. Zeitschr.* 1885) have totally failed to understand these

changes, their accounts of the origin of the aggregated Salpæ have no permanent value.

I pointed out in 1886 ('Studies from the Biol. Lab., Johns Hopkins Univ.,' 1886, pp. 398-414) that the Salpa chain is morphologically a single row of Salpæ, all in the same position, with their dorsal surfaces proximal or towards the base of the stolon and their right sides on its right. The account of the origin of the aggregated Salpæ which is given in this memoir is simply an amplification and expansion of the statement which in 1886 I made briefly and in outline.

The stolon is bilaterally symmetrical, its plane of symmetry is fundamentally identical with that of the solitary Salpæ, and the rudiment of each aggregated Salpa is bilaterally symmetrical in the same plane, although the secondary changes begin very early, and convert the single row into a double row, which comes to consist of a series of right-hand Salpæ and a series of left-hand ones placed with their dorsal surfaces out, their ventral surfaces towards the ventral surfaces of those in the opposite row, and with the left sides of those on the right and the right sides of those on the left towards the base of the stolon. In order to illustrate these secondary changes of position, let us represent the series of Salpæ by a file of soldiers, all facing the same way. Now imagine that each alternate soldier moves to the right and the others to the left, to form two files, still facing the same way. Now let them face about, so that the backs of those in one row are turned towards the backs of those in the other row. They will now represent two rows of Salpæ in their secondary positions.

To make the illustration more perfect, suppose that, instead of stepping into new places the soldiers grow until they are pushed out by mutual pressure, and suppose that their heads, growing fastest, form two rows, while their feet still form one row, and suppose furthermore that, as each soldier rotates, his feet turn first, and that the twisting runs slowly up his body to his head, which turns last. We must also imagine that these various changes all go on together, and that while they are taking place each soldier not only grows larger but also develops from a simple germ to his complete structure.

Salensky regards the stolon as two rows of rudimentary Salpæ; and while Seeliger correctly states that they at first form a single row, he has failed to discover the rotation, and believes that they arise on the stolon in their final positions, and he has therefore failed as completely as Salensky in his efforts to trace the origin of their organs.

The Ectoderm of the Salpa Embryo.—At an early stage of segmentation some of the blastomeres move upwards and pass out of the follicle on the middle line of the dorsal surface, where the two layers of the follicle are continuous with each other. I have given reasons for believing that this is the spot which was once occupied by the blastopore. These ectodermal blastomeres thus become extra-follicular, although they are covered for a time by the capsule of epithelium, which Salensky has called the "Ectodermkeim." They give rise by cell-division to the ectoderm, which spreads from the dorsal middle line downwards and outwards over the embryo, pushing off and replacing the cells of the capsule. The ectoderm has a growing edge, like that of meroblastic embryos, and it does not close in completely on the ventral middle line until after birth.

Salensky ("Neue Untersuchungen," Mitth. a. d. Zool. Station zu Neapel, i., 1882) has figured the migration of blastomeres to an extra-follicular position on the dorsal surface of the embryo in several species, although he regards them as discarded blastomeres and derives the ectoderm from other sources. They are clearly shown in *Salpa pinnata* in his plate xii. fig. 26, in *Salpa pectinata* in his pl. xxiii., and in *Salpa fusiformis* in his plate xxiv. fig. 3, where they are marked by the letters *Eckb*, which might be supposed to stand for "ectodermal blastomeres" if he did not tell us explicitly on p. 389 that the ectoderm of this species is derived from the epithelial capsule ("Epithelhügel").

The ectodermal blastomeres seem to be more conspicuous in *Salpa fusiformis* than in other species, for Salensky says (p. 345) that while the epithelial capsule ("Ectodermkeim") is generally separated very sharply from the embryonic cell-mass, it is at one end of the embryo so intimately related to the follicle cells ("gonoblasts") that it is difficult to determine the boundary between them, and the blastomeres which lie directly at this spot are covered only by the epithelial capsule ("Ectodermkeim"). At a later stage he says (p. 350) that the epithelial capsule ("Ectodermkeim") contains cells which differ greatly among themselves in both size and form. Some of them are similar in appearance to the cells of the epithelial capsule, as already described, at an earlier stage, and differ from them only in being more flattened. "The others (*Eckb*) are very much larger and very different in structure, and contain a nucleus which is very similar to that of the blastomeres. The appearance of these cells suggests that they are blastomeres which have passed out from the cell-mass."

Salensky believes that the ectoderm of *Salpa democratica* is

derived from the oviduct, and that in all other species it is derived from the epithelial capsule ("Epithelhügel," "Ectodermkeim"); but I think all will agree that his position is untenable until he has traced the history of these extra-follicular blastomeres and has proved that they take no part in its formation.

I have shown that they do give rise to the ectoderm and that the epithelial capsule is a transitory structure which is lost as the ectoderm replaces it.

The Ectoderm of the Stolon and that of the Aggregated Salpæ.—All agree that the ectoderm of the stolon is derived directly from the ectoderm of the embryo. In one minor point my observations show that the older accounts are incorrect. It is usually stated that the ectoderm of the stolon is *pushed* out into a tube by the growth of the other constituents of the stolon, and Seeliger says ("Die Knospung der Salpen," Jena. Zeitschr. 1885, p. 13) that it is an evagination ("Ausstülpung") from the ectodermal epithelium of the embryo. This is not literally true, for the ectoderm itself takes a most active part in the formation of the stolon. This is marked off on the body of the embryo by a fold of ectoderm, which pushes backwards from its tip to its base, so that it is folded off from the body of the embryo rather than pushed out, and, in the young stages of *Salpa pinnata* at least, its differentiation from the body of the embryo is chiefly due to the active growth of this ectodermal fold.

The ectoderm of the aggregated Salpæ has been correctly held to be directly derived from the ectoderm of the stolon by all students except Todarro. My own observations show also that the multiplication of the ectoderm cells is the chief agent in the segmentation of the stolon, that the nerve-tube and the perithoracic tubes are cut up into vesicles by the growth of the ectodermal folds, and that these are the chief agents in the segmentation of the endodermal tube and the genital rod.

The Nervous System of the Embryo.—Little can be said of this without illustrations. The caudal nervous system is represented by scattered blastomeres, which soon degenerate and disappear. The ganglion is formed as an invaginated fold of the somatic layer of the follicle, and the ganglionic blastomeres pass into it from the ectodermal ridge and become completely folded in among the follicle cells. The ganglionic rudiment soon loses its connexion with the somatic layer and unites with the visceral follicle cells in the region of the roof of the anterior end of the pharynx.

The Nerve-Tube of the Stolon.—This is formed from the ectoderm on the middle line of the upper surface of the stolon

at the point where its ectoderm folds upon itself to become continuous with that of the embryo. The straight stolon of *Salpa pinnata* is so favourable for studying its origin, and the evidence that it is ectodermal is so simple and clear in this species, that it does not seem necessary to devote much space to the discussion of the observations which have been made on twisted stolons like that of *Salpa democratica*, where it is very difficult to study the young stages by sections. The connexion between the nerve-tube and the endoderm is shown only by very young stolons and for only a short time, and the two structures are quite independent in older stolons.

Of the various writers on the subject, Kowalevsky ("Beiträge," &c, Nachr. d. k. Gesellsch. der Wissensch. zu Göttingen, 1868, 19) seems to regard it as mesodermal in origin. Salensky, in his paper on the budding of *Salpa* (Morph. Jahrb. 1877, iii.), says nothing about its origin. Todarro ('Sopra lo sviluppo,' &c., 1875) derives it, as he does all the other organs of the stolon, from a single germoblastic cell; but I have already shown that his germoblastic cell is a migratory placenta-cell, and all recent writers have justly rejected his account of the stolon. Seeliger believes that in the stolon of *Salpa*, and also in the buds from the ascidiozooids of *Pyrosoma*, it is mesodermal in origin, and that it is derived from an indifferent mass of mesoderm, which, in the young stolon, fills all the space between the ectoderm and the endodermal tube, and becomes differentiated into the nerve-tube and other organs of the stolon.

I have not found at any stage anything in the straight simple stolon of *Salpa pinnata* corresponding to his indifferent mesoderm, although I have studied it in serial sections in the three rectangular planes, and I do not hesitate to affirm that Seeliger has been misled through the selection of a most unfavourable species.

As I have not myself studied *Pyrosoma*, I am not in a position to make any comment on his account of this animal, although Salensky ("Embryonalentwicklung der *Pyrosoma*," Zool. Jahrb. v., 1891) has recently shown that the ganglia of the four primary ascidiozooids which are produced from the stolon of the cyathozooid, as well as the ganglion of the cyathozooid itself, are derived from the ectoderm.

The Ganglia of the Aggregated Salpæ.—The nerve-tube arises as a solid rod, but it soon acquires a lumen. As the ectodermal folds grow inwards and mark out the bodies of the *Salpæ* they cut the tube up into a series of ganglionic vesicles, one for each *Salpa*, with cavities which are segments of the

lumen of the tube. The presence of the ectodermal folds and the growth of the ganglia soon cause crowding and pressure, and the ganglion becomes flattened in the axis of the stolon and elongated transversely. As the oral ends of the pharyngeal pouches grow up to the level of the ganglion, and push in between it and the ectoderm, the crowding becomes still greater and the single series of ganglia breaks up into two rows, which move to the right and left alternately as they grow, and the ganglion of a right-hand Salpa soon comes to lie far away from that of the left-hand Salpa with which it was at first in contact. It is convenient to speak of this change as a "migration" of the ganglion; but there is actually no migration, for the ganglion of each Salpa lies from the first in its final position on the middle line, dorsal to the oral end of the pharynx, and the apparent migration is the result of secondary changes in the position of the bodies of the Salpæ, and is not due to any change in the relation of the ganglion to other organs of the body.

Both Salensky and Seeliger have figured and described the "migration" of the ganglion; but as they have failed to discover the rotation of the bodies of the Salpæ, they regard it as an actual migration, and have completely misunderstood its true relation to the other organs of the body.

My sections show that the "subneural gland" or "ciliated funnel" is an outgrowth from the pharynx and that its intimate relation to the ganglion is secondary. Seeliger believes that the ganglionic rudiment gives rise to both the ganglion and the ciliated funnel, although he admits (p. 20) that his observations are not conclusive.

The Perithoracic Tubes and the Atrium or Cloaca of the Salpa Embryo.—It is not possible to describe the history of these structures intelligibly without figures. They arise as involutions of the somatic layer of the follicle, and they attain to their final form before the blastomeres begin to replace the follicle cells; so that there is a stage when the complete perithoracic system is outlined in cells which do not come from the fertilized egg, but from the follicle.

This system makes its appearance, as it does in the embryos of ordinary Tunicata, as a pair of lateral perithoracic invaginations, although in the Salpa embryo these are formed from the somatic layer of the follicle. They push inwards, penetrate the visceral mass of follicle cells, and meet and unite on the middle line to form the median atrium or cloaca. From the level of the median atrium each perithoracic tube pushes downwards to the region where the cavity of the pharynx is subsequently to be hollowed out in the visceral mass. The

two tubes soon lose their communication with the exterior, and the median cloacal aperture is an independent opening which is formed later. After the pharynx is formed each perithoracic tube unites with it to form a gill-slit. Finally, after the perithoracic system is completely outlined its follicular cells degenerate and are gradually replaced by blastomeres.

Our knowledge of the perithoracic system of *Salpa* in both the solitary and the aggregated form is in great confusion.

Salensky has described the origin of the "gill" and of the median atrium or cloaca of the embryo in a number of species; but the reader of his papers will search in vain for any basis of comparison with other Tunicata, or even for any fundamental unity in his account of the various species of *Salpa*, and his papers contain internal evidence that he has misinterpreted his observations.

Uljanin holds that the perithoracic structures of *Doliolum* are not homologous with those of the ascidian, and Salensky holds the same view regarding *Salpa*. He says that the "gill" is part of the body-cavity which is shut in by folds in the walls of the pharynx, and that the cloaca is not an independent chamber, but a part of the pharynx which is shut off by these folds. A careful study of his description, especially pages 119, 200, 224, 225, and 229 of his first paper, and pages 114, 139, 160, 163, 338, 339, and 354 of his second paper, will show that his views not only involve this conclusion, but that they would also force us to believe that the "gill" and cloaca of one species of *Salpa* are not homologous with the same structures in another species; for his account of their origin in *Salpa democratica* and *Salpa pinnata* has almost nothing in common with his account of them in *Salpa africana*, *Salpa pectinata*, and *Salpa fusiformis*.

In his first paper on *Salpa democratica* he says that, like Leuckart, he regards the gill as part of the inner mantle or branchial sac, that in origin it is nothing more than a strongly developed ridge or thickening on the middle line of the dorsal surface of the pharynx, and that on each side of it the cavity of the pharynx is pushed upwards to form a pair of pouches, which soon meet and unite above the cloaca. In this way the gill-ridge is transformed into a rod, and the rod, which is at first solid, becomes tubular by the conversion of its axial cells into blood-corpuscles.

In this account of the origin of the perithoracic structures of *Salpa democratica* the only point of agreement with my own observations on *Salpa pinnata* is his statement that the gill is at first solid, and that its central cells are set free as development progresses. In his second paper he retracts this

statement, and says (p. 139) that while his studies of the embryo of *Salpa pinnata* have in other respects confirmed his account of the origin of the cloaca and gill of *Salpa democratica*, they show that the gill is in its origin a hollow diverticulum from the body-cavity. He here describes the cloaca and gill as arising in a totally different way in *Salpa africana* (pp. 160 and 163), *Salpa punctata* (pp. 338, 339), and *Salpa runcinata* (*fusiformis*) (p. 354); for while he says that in these species, as in *Salpa democratica* and *Salpa pinnata*, the cloaca is part of the pharynx, it is separated off by two folds (Taf. xxiv. figs. 7 and 8, *Kestp*) of its lateral walls, which grow towards each other and unite on the middle line to form a horizontal diaphragm, which shuts off the dorsal cloacal division of the pharynx from the ventral chamber. The diaphragm then becomes separated at its sides from the lateral walls of the pharynx, so that a secondary communication is established on each side between the upper and the lower chamber, while the middle portion of the diaphragm becomes the gill.

It will be seen that, according to this account, the "gill" of *Salpa democratica* and *Salpa pinnata* arises as an unpaired median dorsal fold, while he describes it in the other species as arising from a pair of lateral folds; in the first two species the gill-slits or openings by which the two chambers communicate at the sides of the gill are primary, while in the others they are secondary; in the first two the cloaca is a secondary chamber formed by the union of the two pouches from the pharynx, while in the other species it is primary.

It does not seem possible to reconcile these statements with each other, and any attempt to bring all or any of them into accord with my own account seems hopeless. More critical examination will show, however, that his observations are rather imperfect than inaccurate, and that his errors are errors of interpretation.

My own observations show that the perithoracic tubes and atrial chamber are formed before the cavity of the pharynx is hollowed out in the mass of visceral follicle cells, and Salensky has, in these early stages, mistaken them for the pharynx or "primitive digestive cavity." This is well shown by the comparison of the two longitudinal sections of embryos of *Salpa runcinata* which are shown in his plate xxiv. figs. 4 and 9). These figures show clearly that the so-called "Darmhöhle" (*Pmd*) of the younger embryo is the cloaca, and not the pharynx of the older one. This is proved even more conclusively by comparing his fig. 3 of plate viii. with fig. 5, for the chamber which is marked *Pdmh* in the younger

embryo is obviously the one which is marked *Kl* in the older one.

The perithoracic tubes are actually shown in many of his figures, notably in his plate vi. fig. 5, *pin*, where they are marked *Drn*. They are also shown in his plate xii. fig. 24, at *Dh*, and their union on the middle line to form the cloaca is shown at *D* in his fig. 25 and at *D* and *Dh* in his fig. 28 A. In the series of sections on his pl. xiii., fig. 31 A shows the two perithoracic tubes cut above the level of the atrium. His figs. 31 B and 31 C show the atrium, and his fig. 31 D shows the two tubes below the level of the atrium but above the level of the pharynx.

Salensky regards these structures as the halves of the primitive digestive cavity, which, he says (p. 114), arises in *Salpa pinnata* as two independent and completely separated halves; and he describes the atrium and gill as arising at a very much later stage in the way which is represented in his plate xiv. fig. 37, and plate xv. fig. 39.

In his plate xxiv., fig. 1 appears to be a section through one of the perithoracic tubes (*Pmdh*) before it has lost its connexion with the surface, and in his description of this figure (p. 346) he says that the triangular primitive digestive cavity is united above to the epithelial capsule ("Ectodermkeim"), and on both sides of the tip are the reflections of the somatic layer of the follicle (follicular wall) already noted, where this passes over into the visceral (gonoblastic) layer.

Salensky correctly describes the manner in which the perithoracic structures (primitive digestive cavity) acquire their first epithelial lining by the migration of the somatic layer of the follicle (follicular wall), and I believe that I have now carried the analysis of his observations far enough to prove that they contain internal evidence of the correctness of my own account.

The History of the Perithoracic Structures of the Aggregated Salpa.—The rudiment of each chain *Salpa* contains two perithoracic vesicles, a right one and a left one, derived from the right and left perithoracic tubes of the stolon. These vesicles give rise to the perithoracic system and to nothing else. Throughout its whole history the perithoracic system is bilaterally symmetrical, although this symmetry is hidden by the changes which take place in the position of the plane of symmetry during growth.

As the right and left pharyngeal pouches are formed the perithoracic vesicles are folded inwards by the growth of the ectodermal folds of the stolon, so that each one of them lies on the proximal or dorsal surface of its corresponding pha-

ryngeal pouch. While the vesicles are hollow from the first, they have at first no communication with the cavities of the pharyngeal pouches. The first trace of the gill-slit is a fold or diverticulum in the dorsal wall of the pharyngeal pouch. This elongates and soon unites with the wall of the perithoracic vesicle to form a gill-slit. Soon after these are formed the posterior ends of the bodies of the Salpæ begin to push out to the right and left in such a way that the elliptical cross section of the body becomes converted into a wedge, with its narrow edge on the left side of a right-hand Salpa, and on the right side of a left-hand Salpa. The two perithoracic vesicles are differently affected by this change, for while the one nearest the pointed end of the wedge is compressed in the line of the axis of the stolon, the other is not. Thus the left perithoracic vesicle of a right-hand Salpa and the right one of a left-hand Salpa become flattened and elongated towards the middle line, while the other remains more nearly circular in section. Their relations to the morphological middle plane are fundamentally identical, but as the middle plane itself gradually moves outwards there is an apparent asymmetry.

Each perithoracic vesicle now becomes extended towards the middle line, where they unite to form the median atrium or cloaca, to which they contribute equally, although the position of the body is such that sections transverse to the long axis of the stolon might easily be misinterpreted and held to prove that the whole median atrium of a right-hand Salpa arises from the left vesicle alone, and that of a left-hand Salpa from the right one alone. The secondary changes of position are, however, of such a character that it is impossible to describe them in detail without figures.

Seeliger's account of the perithoracic structures of *Salpa democratica* (pp. 18, 48, and 63) serves to show how difficult the study of a simple structure may be made by a slight change of position, for phenomena which can be observed with ease in the straight stolon of *Salpa pinnata* are so obscure in *Salpa democratica* that all the industry and technical skill which Seeliger has devoted to this species has had very little outcome.

His account of the history of the perithoracic system is essentially as follows:—The perithoracic tubes, which he calls the "Seitenstränge," are mesodermal in their origin, and are specialized out of a mass of mesoderm cells which gives rise also to the nerve-tube of the stolon and to the genital rod. The mesoderm passes into the stolon from the body of the embryo in an unspecialized condition, and gradually becomes

differentiated into these organs after the stolon is formed. The folds in the ectoderm of the stolon divide the "Seitenstränge" into a series of solid masses at the sides of the stolon between the ectoderm and the endoderm. These bodies are equal in number to the future Salpæ, and not twice as numerous. As each Salpa is constricted off from the tube it carries with it the greater part of one of these masses of cells from one side of the stolon and the lesser portion of the one on the opposite side. These two masses are not bilaterally placed in the body, but are on the middle line, the larger one being dorsal or neural and the smaller one ventral or hæmal. The latter gives rise to the heart and to the eleoblast, while the larger one, on the neural surface, gives rise to most of the mesoderm of the chain Salpa and also to a cloacal vesicle which is median and unpaired.

The vesicle becomes distended, and at two points, one on each side of the middle line, it unites with the wall of the branchial sac, and the cloaca and the branchial chamber thus become connected through the two gill-slits, while a similar union with the ectoderm in the middle dorsal line forms the cloacal aperture. Seeliger's account is perhaps as near the truth as one could hope to get by the study of transverse sections of the twisted stolon of *Salpa democratica*; but a very little study of sections in other planes in more favourable species will show that he has completely failed to understand the subject and that his account has no permanent value.

It is not only irreconcilable with my own observations, but also with our knowledge of *Pyrosoma*, for both Seeliger ('*Pyrosoma*,' pp. 622-624) and Salensky ('*Pyrosoma*,' pp. 31-36) state that in this genus the perithoracic system is bilaterally symmetrical, that each bud has two perithoracic vesicles, which are not dorsal and ventral, but right and left, that each of them unites with its own side of the pharynx to form the gill-slits before the two vesicles unite with each other to form the median atrium, and that this arises, as it does in the aggregated Salpa, on the dorsal middle line by the meeting and union of diverticula from the two vesicles, and that the external aperture arises still later, as it does in Salpa, as an independent aperture on the middle line.

The perithoracic vesicles are derived, as I find that they are in Salpa, from the right and left perithoracic tubes of the stolon; but, in the primary ascidiozooids at least, these are continuous with the perithoracic tubes of the primary embryo or cynthozoid, where, according to both Kowalevsky and Salensky (pp. 466, 473-475), the evidence that they arise as

paired ectodermal invaginations from the surface of the body is clear and unmistakable.

The Digestive Organs of the Embryo.—The cavity of the pharynx arises in the mass of visceral follicle cells by the degeneration of these cells. Its endodermal epithelium is derived from the blastomeres, and the gut is formed later as a diverticulum from the pharynx.

Salensky's account of the origin of the digestive organs is scattered through the pages of his memoir in such a way that it is hard to review; and as I have shown that he has in the youngest embryos mistaken the two perithoracic tubes for the pharynx, that he has at a somewhat older stage mistaken the median atrium or cloaca for the pharynx, and that he has failed to discover the actual pharynx during its early stages, it is clear that his description has no value.

The Endodermal Tube of the Stolon and the Digestive Tract of the Aggregated Salpa.—The endodermal tube of the stolon is formed as a diverticulum from the ventral middle line of the pharynx of the solitary Salpa, and its communication with the cavity of the pharynx is retained throughout the whole history of the stolon. The thickened side-walls of the endodermal tube are derived from the two endostylic folds of the pharynx of the embryo.

The pharynx of the aggregated Salpa is morphologically bilaterally symmetrical with the middle plane of the stolon, although this fact is obscured by the secondary changes of position. It is formed from two pharyngeal pouches, a right and a left, from the sides of the endodermal tube of the stolon. The oral ends of these pouches grow forwards and quickly meet and unite on the morphological middle line to form the oral end of the pharynx. The aboral ends grow backwards and approach each other on the middle line, and finally unite, although they remain separate very much longer than the oral ends.

In a strict sense the pharynx is not actually, but only apparently double in origin, for the middle section or endodermal tube is not double. Fundamentally it is a single unpaired expansion of the endodermal tube, but at the time when it elongates towards the oral and aboral ends of the body the middle line is occupied by the blood-tubes, and it pushes along the sides of these structures, and does not become complete in the middle line until a much later stage.

The post-pharyngeal gut arises as a blind diverticulum from the aboral end of the right pharyngeal pouch. The part of the diverticulum nearest the pharynx becomes the

oesophagus, and the stomach and intestine are developed from its blind end. In all the species I have studied the intestine bends to the left past the stomach, to open dorsally into the median atrium, and the digestive tract assumes the form of a figure 8, which is persistent in most species, although in *Salpa pinnata* the intestine gradually moves downward as development advances, until it finally becomes ventral to the stomach.

As the gut arises, in both right-hand and left-hand Salpæ, from the right pharyngeal pouch, and since the distortions which are produced by pressure and by the changes of position affect the right-hand pouch of a right-hand Salpa just as they affect the left-hand pouch of a left-hand Salpa, and since they affect the other pouches in quite a different way, the history of the gut in a right-hand Salpa is superficially very different from that of a left-hand Salpa, although fundamentally they are exactly alike.

While Salensky, in his first paper on the budding of Salpa, describes the endodermal tube, he says that it takes no part in the construction of the Salpæ, and that their digestive organs are derived from that part of the stolon which I have called the genital rod. Seeliger, a few years later, pointed out Salensky's error, which he has himself admitted in a recent paper ('Pyrosoma,' p. 78).

Seeliger's account of the origin of the endodermal tube and digestive organs is given on pp. 14, 18, 26-34, and 54-62 of his paper on the budding of Salpa. He shows (p. 14) that the endodermal tube of the stolon is derived from the pharynx of the embryo, with which it at first communicates, although he says that this connexion is soon lost; while my observations show that it is persistent at all stages in the history of the stolon of *Salpa pinnata* and *Salpa cylindrica*.

He gives (p. 18) a good description of the segmentation of the side-walls of the endodermal tube, but he says that the endoderm and mesoderm are the active agents in the segmentation of the stolon; while my own observations show clearly that the most active agent is not the endoderm nor the mesoderm, but the ectoderm.

He states correctly that the structures which I have called the pharyngeal pouches arise from the side-walls of the endodermal tube, and that two of them enter into the body of each Salpa; but here the agreement between his account and my own observations ends, although his figures show clearly that the species which he studied, *Salpa democratica*, agrees in all essentials with those which I have studied.

While the two pharyngeal pouches are actually right and left, he regards one as dorsal and the other as ventral, and

says that the dorsal one is largest and that it lies from the first on that side of the stolon to which the Salpa belongs, and that it runs through the whole length of the body of the young chain Salpa and opens in its middle region into the horizontal endodermal tube of the stolon, so that a neural and a hæmal part are distinguishable.

His account and figures show that his so-called dorsal pouch is actually the right pouch of a right-hand Salpa or the left pouch of a left-hand one.

In other respects his account of the origin and primary relations of this pouch is correct, although he fails to discover that the history of the second pouch is exactly the same.

He describes the second pouch as ventral and much smaller and as lacking the oral end, and he says that it looses long before the dorsal pouch its connexion with the horizontal tube, and becomes a closed vesicle, and that, as the hinder ends of the bodies of the Salpa diverge from each other, the smaller ventral pouch pushes further backwards than the larger dorsal one, and that the hindermost end of the dorsal pouch gives rise to a diverticulum which grows round the hinder surface of the ovary to unite with the ventral pouch. The dorsal pouch gives rise, he says, to the pharynx, on the ventral surface of which the endostyle is developed, while the œsophagus, stomach, and intestine are formed from the rudiment which has arisen at the posterior end by the union of the two pouches.

It is not necessary to enter into a more minute analysis of his description, for comparison will show that he has been misled by his erroneous conception of the primary position of the buds, and has mistaken the symmetrical right and left pouches for unpaired dorsal and ventral ones.

His more recent account of the origin of the post-pharyngeal gut of *Pyrosoma* ('*Pyrosoma*,' pp. 23-25) is very similar to what I have found in Salpa; for he says (pp. 615-622) that while it arises as a pair of folds from the pharynx, these soon unite to form an unpaired diverticulum, which afterwards becomes differentiated into œsophagus, stomach, and intestine; that its pharyngeal end becomes the œsophagus, while the intestine arises from its blind end and ultimately acquires an anal opening into the median atrium.

Salensky's account of the origin of the gut in *Pyrosoma* is quite different, however, for he says ('*Pyrosoma*,' pp. 69-72) that it is bilateral in origin and arises as a pair of folds from the sides of the aboral end of the pharynx, which unite with each other to form a horseshoe-shaped canal. If I understand his description, he holds that the right fold forms

the œsophageal portion of the gut and the left one the intestinal portion, and that both open at first into the pharynx, although the intestine soon looses this connexion and acquires a new anal opening into the median atrium.

Baltimore,
April 25, 1893.

XXV.—*Descriptions of Three new Species of the Genus Iletica* (Cantharidæ) *in the Collection of the British Museum.* By Mrs. M. K. THOMAS.

[Plate VI. B. figs. 1-3.]

Iletica Waterhousei, sp. n. (Pl. VI. B. fig. 2.)

Head narrowed in front, deeply impressed in the centre; anteriorly black and more finely and thickly punctured than posteriorly, where it is red-brown, glabrous, and very shining; eyes brown; palpi and labrum reddish; antennæ black.

Prothorax red-brown, with black down its centre, broader than long, its outer sides slightly convergent posteriorly; a strongly defined posterior transverse impression; a deep median groove with two foveæ on either side, one large and deep, placed posteriorly, the other small and fainter, situated further forwards and outwards; slightly pubescent anteriorly, glabrous and very shining posteriorly.

Scutellum black, finely punctured and shining.

Elytra half as broad again as the prothorax, long, rather rugose, each elytron with four slightly raised lines, including the sutural ones; anterior halves of elytra deep yellow, with two bands of black, their posterior halves wholly black.

Underside and *legs* covered with short yellow pubescence, the former black with yellow patches on the metasternum, the latter black with red spots on the femora of the posterior pair; abdominal segments yellow and infuscated.

Length 32, breadth 10 millim.

Hab. Sierra Leone (*Coll. Foxcroft*).

Besides the type there are in the British Museum two other specimens which, although they vary somewhat as to coloration, are in all other points so similar to *I. Waterhousei*, that they should apparently be referred to the same species. One is of unknown locality, the other also comes from Sierra Leone.



Brooks, William Keith. 1893. "XXIV.—The origin of the organs of Salpa." *The Annals and magazine of natural history; zoology, botany, and geology* 12, 123–138. <https://doi.org/10.1080/00222939308677593>.

View This Item Online: <https://www.biodiversitylibrary.org/item/78509>

DOI: <https://doi.org/10.1080/00222939308677593>

Permalink: <https://www.biodiversitylibrary.org/partpdf/62274>

Holding Institution

University of Toronto - Gerstein Science Information Centre

Sponsored by

University of Toronto

Copyright & Reuse

Copyright Status: NOT_IN_COPYRIGHT

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.